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Number-Theoretic Properties of Two-Dimensional Lattices*, †

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The notion of visible point in a lattice is extended to the notion of visible pair of points in a two-dimensional infinite lattice, normalized as a vertical strip of width 1, centered at the origin. The pair (m, n) is shown to be visible iff $|m(nd) - n(md)| = 1$, where (x) is the integer nearest to x, d (a value between 0 and $\frac{1}{2}$) is the abscissa of point 1, while $xd - (xd)$ is that of point x. A general characterization of the visible and opposed pairs (with respect to the vertical axis of the lattice) will be put forward. Geometrical and computational algorithms delivering all the visible pairs for any value of d will be presented. The biological meanings of these and other results will be mentioned.

1. Introduction

This article presents original properties of regular point lattices emerging from an application oriented view point. It introduces Farey sequences for the treatment of basic current objects in phyllotaxis, the part of botany concerned with the genesis of the patterns of primordia (e.g., leaves, florets, scales, seedlings) observed on plants and in buds.

When a plant is observed, spirality catches the eyes, such as for the capituli of the daisies and the surfaces of the pineapples, where two families of opposed parastichies (spirals) are conspicuous. The cylinder-like pineapple with its helices and the disk-like daisy with its parastichies become, by a mathematical transformation, families of straight lines in a lattice of points representing the centres of the primordia (the florets of the daisy, the

* The article is dedicated to L. and A. Bravais, the French botanist and his brother a mathematician, who initiated one hundred and fifty years ago the lattice treatment of phyllotaxis.

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scales of the pineapple). Joining any two points x and y of the lattice determines a direction and thus a family of $m = |x - y|$ parallel, equidistant straight lines (unfolded helices) partitioning the points of the lattice and linking them from m to m. Any two such families containing respectively m and n lines is denoted by (m, n). When the lines in a family have a positive slope while those in the other have a negative slope we say that the pair (m, n) is opposed. The pair (m, n) is said to be visible when there is a point of the lattice at every intersection of two lines in the pair. For example, in Fig. 1 the pair (5, 7) is opposed given that 7 and 5 appear in "opposite" strips, one with abscissa between $-\frac{1}{2}$ and 0, the other with abscissa between 0 and $\frac{1}{2}$. The pair is not visible since the line going through the points 7, 14, 21, 28, ..., does not meet the line going through the points 5, 10, 15, 20, ..., at a point of the lattice. The pair (5, 13) is neither opposed nor visible. The pair (5, 14) is not opposed but it is visible. The pair (17, 4) is visible and opposed.

The notion of visible pair (of spirals) is current in phyllotaxis, but in the theory of Farey sequences only the notion of a visible point in a lattice is found. We will see that the former generalizes the latter, and obtain by doing so a new definition of the former to replace the one given above due to Adler [1]. Propositions 1 and 2 give an original number-theoretic characterization of the visible pairs, while Proposition 5 gives a characterization of the visible opposed pairs. Proposition 5 is based on

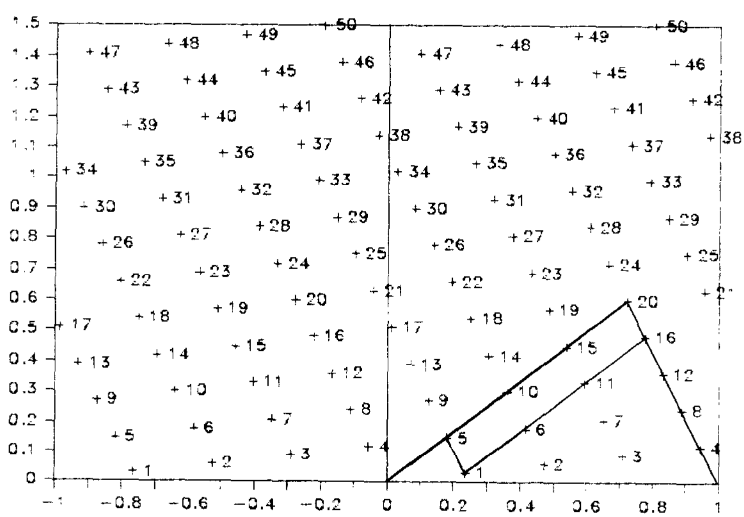

FIG. 1. Lattice built with the value $d = 17/72$. The coordinates of the multiple representations of point n are $(nd\text{-}m, nr)$, where m is any integer. In the vertical strip S the coordinates of point n are $(nd\text{-}(nd), nr)$. See the example before Proposition 4 for a discussion of the triangles in the figure.

Proposition 1, and the examples at the end of the paper show how easily the visible pairs are obtained, graphically and mathematically. The theory done here concerns lattices from a general point of view, but we will briefly see how the results can be particularized to obtain the current series of integers, divergence angles, and results of phyllotaxis. The developments around Proposition 8 drive us to the core of an important trend in phyllotaxis, put forward by Bravais and Bravais [2], in which Coxeter [3] provided a meaningful contribution obtained here as a particular case.

The paper does not attempt to present the biological nature of phyllotaxis. It is not designed to bridge the gap between strictly botanical phyllotaxis and mathematical phyllotaxis. It shows how Farey sequences delve into the spatial relationships among leaf primordia, represented by lattices of points. For an access to the literature on phyllotaxis and related subjects, see, for example, Jean [6]. Appendix I shows briefly how lattices of points can be seen to evolve from the study of phyllotaxis.

2. Preliminary Notions and Notations

Figure 1 shows a lattice similar to the ones obtained in the study of phyllotaxis. The lattice is made with a divergence d of $85°$ or $85/360 = 17/72$. This is the angle between consecutively born primordia, that is the abscissa of point 1 in the regular lattice, a number always taken to be smaller than $\frac{1}{2}$. The coordinates of point n, $n = 1, 2, 3, \ldots$, are $(nd - m, nr)$ where r, called the rise, is the ordinate of point 1, and m is an integer. We will concentrate on the infinite vertical strip, denoted by S, of the points whose abscissae are between or equal to -0.5 and $+0.5$. In this sector of the lattice the coordinates of point n are $(nd - (nd), nr)$, where (nd) is the integer nearest to nd. If nd is half an odd integer, (nd) is allowed to be either $[nd]$ or $[nd] + 1$ where $[nd]$ is the integral part of nd. The value $nd - (nd)$ is called by botanists the secondary divergence of point n. For any given integer N, the ordered set of fractions $(kd)/k$, $k = 1, 2, 3, \ldots, N$, in their lowest terms, will be denoted by A. The fractions in A are smaller than $\frac{1}{2}$. The past analyses (e.g., Coxeter [3], Adler [1], Marzec and Kappraff [11]) are performed in the region of the lattice with abscissae between 0 and 1.

The closer point x is to the vertical axis, the closer the value $(xd)/x$ is to d. The fraction is called a phyllotactic fraction, an approximation of d. Bravais and Bravais knew how to determine phyllotactic fractions from plants (see Jean [8]). Enrolling the vertical strip S to form a cylinder, (xd) represents the number of turns on the helix around the cylinder to reach x from 0 through the consecutive points $1, 2, 3, \ldots$, by the shortest path from 0 to 1. Moreover two points x and y on each side of the vertical are such that d is between $(xd)/x$ and $(yd)/y$.

The text often mentions the general relation $|m(nd)-n(md)|=1$ for the visible pair (m, n) on a plant with divergence d. This important relation in phyllotaxis, under a slightly different though equivalent form, has been discussed by many botanists such as Thomas, Thornley, Richards and Erickson (see Jean [6] for references). This relation concerns the observation according to which the numbers in the pair (m, n) are generally *consecutive* terms of the Fibonacci series 1, 1, 2, 3, 5, 8, 13, ..., called the Main series by the botanists. The consecutive terms are translated here as consecutive terms of a subsequence A, corresponding to d, of a Farey sequence.

Let m, n, and $m+n$ be three points of the lattice such that they form with the origin a parallelogram having on and inside it no other point of the lattice. This parallelogram is called a fundamental region of the lattice. Translations transform it into infinitely many such regions filling the plane without overlapping and without interstices, and their vertices are all the points of the lattice. The triangle made with the points 0, m, and n can be used just as well to generate the lattice. It is well known that the area of any fundamental region, whether it be a parallelogram or a triangle, is, respectively, the same.

The Farey sequence F_N of order $N=1, 2, 3, \ldots$, is the discrete set of rational numbers p/q, in their lowest terms, between 0 and 1, such that $q \leqslant N$, arranged in increasing order of magnitude. For example, F_4 is the sequence 0/1, 1/4, 1/3, 1/2, 2/3, 3/4, 1/1. These sequences were discovered over a hundred years ago, but their significance in number theory has been revealed only in modern times. The main properties (LeVèque [10]) we will be using are:

1. if p/q and s/t are consecutive in F_N for some N, then $|pt-qs|=1$
2. if $|pt-qs|=1$, then p/q and s/t are consecutive in F_N for

$$\max(q, t) \leqslant N < q+t,$$

and they are separated by the single element $(p+s)/(q+t)$ in F_{q+t}.

The latter element is called the mediant of p/q and s/t.

3. Number-Theoretic Properties of Visible Pairs

Proposition 1. *In the regular lattice with divergence d and rise r, if the points m and n are such that* $|m(nd)-n(md)|=1$, *then the pair* (m, n) *is visible.*

Proof. Consider the points $k=1, 2, 3, \ldots, m$ of S, assuming that m is larger than n. The corresponding ordered set of fractions $(kd)/k$ forms a subsequence A, depending on d, of F_m. Each one of the fractions in A is an approximation of d: the closer the ray from 0 to k is to the vertical axis, the better the approximation is. The ray from 0 scanning the first m points of S, from the positive to the negative horizontal axis, will go through the m points in the proper order of the fractions in A, that is in the order of increasing or decreasing values $(kd)/k$, depending on whether point 1 is on the right or on the left of the vertical axis, respectively (that is depending on the direction of what is called the genetic spiral going through the points 1, 2, 3, ...). Given that $|m(nd)-n(md)|=1$, $(md)/m$ and $(nd)/n$ are consecutive fractions in F_t for $m \leqslant t < m+n$. It follows that in F_t the ray reaches m and n consecutively. The triangle made with the points 0, m, and n is thus a fundamental region. This means that the pair (m, n) is visible. ∎

In some cases (nd) or (md) will have two possible values. But as long as for one of these values the relation $|m(nd)-n(md)|=1$ holds, the pair (m, n) will be visible (see Example 2 in Section 5). The proof of Proposition 1 suggests an equivalent definition for the concept of visible pair. A pair (m, n) is visible if and only if a ray from 0 scanning the first N points of the strip S, where $\max(m, n) \leqslant N < m+n$, meets m and n consecutively. Otherwise stated the pair (m, n) is visible when there is a triangle in S whose vertices are 0, m, and n, and which does not meet and contain another point of the lattice. This concept generalizes the following from Hardy and Wright [4]: a point n of a lattice is said to be visible if the ray from 0 to n contains no point of the lattice between 0 and n. For any given N, the points of S corresponding to A, that is the denominators of the fractions in A, are visible given that the members of A are in their lowest terms.

PROPOSITION 2. *If the pair (m, n) is visible then $|m(nd)-n(md)|=1$.*

Proof. By the alternative definition for the visible pair, m and n are met consecutively by the ray from 0. This means that $(md)/m$ and $(nd)/n$ are consecutive in F_N for $\max(m, n) \leqslant N < m+n$. It follows by a result on Farey sequences that $|m(nd)-n(md)|=1$. ∎

For the pair (m, n), m and n may be relatively prime; that does not mean that (m, n) is visible. For example, in the case of Fig. 1, for the pair $(7, 5)$ there exist integers $u=3$ and $v=2$ such that $|mv-nu|=1$, and we already know that the pair is not visible. Notice in this case that $(7d)=2 \neq u$, $(5d)=1 \neq v$, and that the divergence is between $(5d)/5$ and $(7d)/7$ as expected (given, as we already know, that the pair is opposed), not between $v/n=2/5$ and $u/m=3/7$ as must be the case when the pair (m, n) is visible and opposed, as in Proposition 3.

PROPOSITION 3. *If (m, n) is a visible opposed pair, there exist unique integers u and v such that $0 \leqslant u < m$, $0 \leqslant v < n$, $|mv - nu| = 1$, and such that the divergence $d \leqslant \frac{1}{2}$ lies at or is between u/m and v/n.*

Proof. By Proposition 2 we have that $u = (md)$ and $v = (nd)$ satisfy the requirements $|mv - nu| = 1$, $0 \leqslant u < m$, and $0 \leqslant v < n$. The pair being opposed d is between the bounds $(md)/m$ and $(nd)/n$.

Generally speaking, forgetting the restrictions on u and v, m and n being relatively prime, and the diophantine equation having a solution, it has infinitely many. The restrictions $0 \leqslant u < m$ and $0 \leqslant v < n$ show that there is a finite number of solutions. More precisely u/m and v/n being consecutive in F_N for $\max(m, n) \leqslant N < m + n$, if d is to be between two such consecutive fractions, the choice for u and v is bound to be unique. ∎

The statement of Proposition 3 is already known (from Jean [8]), but the proof given there is carried out on an example such as the following one, and the method of proof, based on the elementary properties of similar triangles, has limited perspectives.

Consider in Fig. 1 the visible opposed pair $(5, 4)$ $(m = 5,\ n = 4)$. The figure shows three triangles, called visible opposed parastichy triangles, whose vertices on their respective bases are on, or near, the horizontal axis, and whose vertices are respectively the points 5, 20, and 16. Those triangles are approximately similar. The first two yield the relations $u/m \leqslant d \leqslant v/n$, and $mv - nu = 1$, where $v = 1$ (step from 0 to 5), and $u = 1$ (step from 1 to 5). In that case notice that d is smaller than $\frac{1}{2}$ as requested. Working with the last two triangles delivers the relations $mv - nu = -1$, and $v/n \leqslant d \leqslant u/m$, where $v = 3$ (steps from 1 to 16), and $u = 4$. But that case does not to a divergence smaller than $\frac{1}{2}$.

PROPOSITION 4. *Suppose that the divergence angle $d \leqslant \frac{1}{2}$ is in the bounds u/m, v/n, where $|mv - nu| = 1$, $0 \leqslant v < n$, and $0 \leqslant u < m$. Then the pair (m, n) is visible and opposed.*

Proof. For definiteness suppose that $u/m \leqslant d \leqslant v/n$. Then $dn - v \leqslant 0 \leqslant dm - u$, meaning that $v = (dn)$, $u = (dm)$, and that m and n are on different sides of the vertical axis. Indeed, from the inequalities and by hypothesis we have that $|dn - v| \leqslant 1/m < \frac{1}{2}$, and $|dm - u| \leqslant 1/n < \frac{1}{2}$, for m, $n = 3, 4, 5, \ldots$. Thus the pair (m, n) is opposed, and by Proposition 1, it is visible. The cases $(1, 2)$, $(2, 3)$ and $(1, 3)$ are easily settled. ∎

PROPOSITION 5. *Let (m, n) be a spiral pair. The following properties are equivalent*:

1. *there exists unique integers $0 \leqslant v < n$, and $0 \leqslant u < m$ such that*

$|mv-nu|=1$ and $d \leqslant \frac{1}{2}$ is in the closed interval whose endpoints are u/m and v/n;

2. *the pair (m, n) is visible and opposed.*

In botany there is what is called normal and anomalous phyllotaxis. The former case is governed by the sequence 1, t, $t+1$, $2t+1$, $3t+2$, ..., whose general term is denoted by $S_{t,k}=f_k t+f_{k-1}$, where f_k is the kth Fibonacci number (so that $f_1=f_2=1$), and where $t=2, 3, 4, \ldots$. A basic result states that $(S_{t,k}, S_{t,k-1})$ is a visible opposed spiral pair if and only if the divergence angle d of the system is equal to $f_k/S_{t,k}$ or to $f_{k-1}/S_{t,k-1}$ or is between those two values. This result, first discovered by Adler [1], is of tremendous importance in phyllotaxis; I gave many applications of it, underlined its historical meaning, provided an intuitive presentation of it, and illustrated it by means of the theory of Antriebes of the botanist Bolle (see Jean [8]). Since $|f_k S_{t,k-1}-f_{k-1}S_{t,k}|=1$, Proposition 5 generalizes this result (put the values $m=S_{t,k}$, $n=S_{t,k-1}$, $v=f_{k-1}$, and $u=f_k$). The divergence corresponding to the sequence of normal phyllotaxis, that is the number in the intersection of the closed intervals given by Proposition 5, is $d=1/t+\phi^{-1}$ where $\phi=(5^{1/2}+1)/2$. Since $S_{2,k}=2f_k+f_{k-1}=f_{k+2}$, the Fibonacci sequence itself is obtained when $t=2$. This arises in about 95% of all the observations. The corresponding divergence angle is ϕ^{-2}, a fraction which when multiplied by 360° gives $137\frac{1}{2}$°, the almost omnipresent puzzling angle observed between the consecutive primordia of plants.

4. Further Properties of the Visible Pairs

If the pair (m, n) is visible then the pairs $(m+n, n)$ and $(m, m+n)$, called the extensions of (m, n), may not be visible given that the point $m+n$ may fall out of the strip S, when forming the fundamental parallelogram with 0, m, and n. For example, in Fig. 1 the pair (5, 19) is visible but the extension (5, 24) is not. The same cannot be said about the contraction of (m, n) as Proposition 6a shows. The contraction of a pair (m, n) is the pair $(m-n, n)$ if $m>n$, and the pair $(m, n-m)$ if $m<n$. Moreover a pair (m, n) may be opposed, but its contraction may be not, as Fig. 1 shows for the contraction (4, 15) of (19, 15), contrarily to what happens when the opposed pair is also visible, as Proposition 6b shows. That a contraction of a visible opposed pair is visible and opposed is already known from Adler [1], working with opposed parastichy triangles in the strip of points with abscissae between 0 and 1; a proof is given here in the strip S. Proposition 6c brings a precision in Adler's [1] where it is said that an extension of a visible opposed pair is not necessarily visible. What is implicitly meant in

fact by this is that the extension is not necessarily visible and opposed. That author only considered visible pairs that were opposed, for the purpose of his particular model. One of the motivations for Propositions 1, 2, 6a, and 6c comes from the possibility of having visible pairs that are not opposed.

PROPOSITION 6. (a) *If (m, n), $m > n$, is visible, its contraction is visible, and*

$$(md) - (nd) = ((m-n)\, d);$$

(b) *if (m, n), $m > n$, is visible and opposed, its contraction is visible and opposed, and*

$$mD_n + nD_m = 1,$$

$$D_m + D_n = D_{m-n},$$

where $D_x = |xd - (xd)|$, $x = n, m, m-n$;

(c) *if (m, n) is visible and opposed, both extensions are visible, at least one of them is opposed, and*

$$D_{m+n} = |D_m - D_n|.$$

Proof. If $m-n$, as one of the vertices of a parallelogram based on the points 0, m, and n, falls inside the strip S, then these four points of S form a fundamental region, and the pair $(m-n, n)$ is visible. Then $(md)/m$ becomes the mediant between $((m-n)\, d)/(m-n)$ and $(nd)/n$ and we get $((m-n)\, d) = (md) - (nd)$. If m and n are on the same side of the vertical axis, or if one of these points is on the axis, the pair $(m-n, n)$ is obviously visible. Let us assume then, without loss of generality, that m and n are on different sides of the axis, and that point 1 is on the right. Proving that $m-n$ is in S amounts proves that $D_m + D_n < \frac{1}{2}$, in which case we clearly get $D_m + D_n = D_{m-n}$. We have $D_m = md - (md)$ and $D_n = (nd) - nd$, or $D_m = (md) - md$ and $D_n = nd - (nd)$. In both cases, by Proposition 2, we obtain $mD_n + nD_m = 1$ (notice that these relations are not true if the pair (m, n) is not opposed).

Suppose next that $m > n \geqslant 3$. Assuming without loss of generality that $D_m \leqslant D_n$, we obtain $(m+n)\, D_m \leqslant nD_m + mD_n = 1$, so that $D_m \leqslant \frac{1}{6}$. Also $mD_n < 1$, and $D_n < \frac{1}{3}$. It follows that $D_m + D_n < \frac{1}{2}$. We only need to settle the cases where m or n, or both, take the values 1 and 2.

If $n = 2$ is on the left side of the vertical axis, we have the hypothesis that $(2, m)$ is visible and opposed, and that $m = 3, 5, 7, \ldots$. Then $(nd) = 1$, $D_n = 1 - 2d$, $2D_m + m(1-2d) = 1$, and $D_m = [1 - m(1-2d)]/2$. It follows that

$$0 < D_n + D_m = \tfrac{1}{2} - (m-2)(1-2d)/2 < \tfrac{1}{2}.$$

Notice that if point 1 is on the right, point 2 cannot be on the right if the pair (m, n) is to be visible and opposed, given that then point 2 is not visible from the origin.

Suppose finally that $n = 1$ is on the right of the vertical axis, and consider the visible opposed pair $(1, m)$, $m = 2, 3, \ldots$. The case $m = 2$ is rejected given that we are considering the contraction of $(1, m)$. We have $(nd) = 0$, $D_n = d$, $D_m = 1 - md$, $(md) = 1$, and $D_n + D_m = 1 - (m-1)\,d$. By Proposition 3, $d < 1/m$. Also, $1 - md < 1/(m-1)$ so that $D_n + D_m < \frac{1}{2}$ for $m = 4, 5, 6, \ldots$. For the case $m = 3$, if 2 is on the right of the vertical, $2d < \frac{1}{2}$, $d < \frac{1}{4}$, $1 - 3d < \frac{1}{4}$, $D_n + D_m < \frac{1}{4} + \frac{1}{4} = \frac{1}{2}$; if 2 is on the left, $\frac{1}{2} < 2d$, $D_n + D_m = 1 - 2d < \frac{1}{2}$. This settles parts (a) and (b) of the proposition. Part (c) is very easily taken care of. ▮

An important sector of phyllotaxis concerns the conspicuous pairs. The visible points m and n such that the Euclidean distances from 0 to m, and from 0 to n, denoted respectively by $d(0, m)$ and $d(0, n)$, are the two shortest possible distances between the points of the lattice, determine what is called a conspicuous pair, denoted by (m, n). Notice that for a given d it is the value of the rise r which determines which pair is conspicuous. It is known that when $d(0, m) = d(0, n)$ the conspicuous pair is visible (see Jean [6, p. 43]). Dropping the restriction $d(0, m) = d(0, n)$ we still have that a conspicuous pair is visible (I. Adler, personal communication, October 7, 1984) but it is assumed that the pair is opposed. By the approach with Farey sequences initiated here, the proof that a conspicuous pair is visible is straightforward. Moreover it is easily proved that a conspicuous pair is opposed. This is the object of Proposition 7.

PROPOSITION 7. *If the pair (m, n) is conspicuous, (m, n) is visible and opposed.*

Proof. The ray from 0 scanning $N = \max(m, n)$ points of the lattice will not meet any other point of the lattice between m and n, inside and on the circle with radius $\max(d(0, m), d(0, n))$, given that m and n are the nearest points to 0. This means that (m, n) is visible.

Suppose now, without loss of generality, that $d(0, m)$ is smaller than $d(0, n)$. We have

$$d(0, m-n) = [d(0, m)^2 + d(0, n)^2 - 2d(0, m)\, d(0, n) \cos\theta]^{1/2},$$

where θ is the angle at 0 determined by m and n. If m and n were on the same side of the vertical in S then, the value of r decreasing, it would become possible to have θ as close as we want to 0 degrees so that

$$d(0, m-n) \simeq d(0, n) - d(0, m),$$

a relation which cannot hold given that m and n are the nearest to 0. ▮

Consider all the points m, n of the lattice such that (m, n) is a visible opposed pair. On each side of the vertical axis, join the points with two infinite polygonal lines. When d is irrational there is no point of the lattice between the two lines, except 0. The relations in Proposition 6 show that the polygonal lines are asymptotic to the vertical axis. The points of the lattice on these lines are called the neighbors of the vertical axis. This definition differs from the one found in Coxeter [3], but it is equivalent. The neighbors of the axis, for d, correspond therein to the points of the square lattice on the lines asymptotic to the line $y = dx$ in Klein's well-known geometric representation of the continued fraction for d. Assuming, as Bravais and Bravais [2] did, that $d < \frac{1}{2}$, that d is an irrational number, and that by going upward along the vertical axis the neighbors of this axis are seen alternately on the right and on the left of this axis, Coxeter's [3] contribution to phyllotaxis was to prove that the divergence d belongs to the set of numbers whose continued fractions do not have intermediate convergents, and consequently that $d = 1/t + \phi^{-1}$, where $t = 2, 3, 4, \ldots$. Proposition 8 gives this result as a particular case.

Proposition 8. *If d is an irrational number smaller than $\frac{1}{2}$, if the pair (m, n), $m > n$, is visible and opposed, and if from n and m the neighbors of the vertical axis indefinitely alternate on each side of it, then*

$$d = [\phi(md) + (nd)]/(\phi m + n).$$

Proof. By Propositions 5 and 6c, by a previously stated result on Farey sequences, and by the hypothesis of alternation, the pairs (n, m), $(m + n, m)$, $(m + n, 2m + n)$, $(3m + 2n, 2m + n), \ldots$, are the only visible and opposed pairs with components larger than m, and d is in every interval of an infinite sequence of closed nested intervals whose length tends toward zero. The intersection of those intervals contains only d, which is given by

$$d = \lim_{k \to \infty} [f_k(md) + f_{k-1}(nd)]/f_k m + f_{k-1} n,$$

and the result follows. ∎

5. Examples and Algorithms

Example 1. *Particular cases of Proposition* 8. Putting $m = t$ and $n = 1$ in Proposition 8, $(nd) = 0$, $(md) = 1$, $d = 1/t + \phi^{-1}$, and we get the sequence $S_{t,k}$ of normal phyllotaxis deduced by Coxeter [3] from Bravais and Bravais' hypotheses. If $t = 2$, the system grows along the Fibonacci series and $d = \phi^{-2}$.

If $n = 2$ and $m = 2t + 1$, $(nd) = 1$, $D_n = 2d - 1$, $D_m = t - d(2t + 1)$ (Proposition 6), and $(md) = t$. Then $d = \frac{1}{2} + 1/t + \phi^{-1}$, $t = 2, 3, 4, \ldots$, corresponding to the cases of anomalous phyllotaxis considered by Jean [9] with the above cases of normal phyllotaxis. The value $t=2$ gives the most current case of anomalous phyllotaxis governed by the sequence 2, 5, 7, 12, 19, 31, ..., and the corresponding angle of approximately 151°.

The set of angles of Proposition 8 were obtained, under a different form of expression, and from other considerations, by Marzec and Kappraff [11], as distributing the leaves around the stem of the plant more uniformly than the neighboring angles can do. The angles do not have intermediate convergents from a certain term, meaning geometrically that the infinite polygonal lines mentioned earlier do not have, from a certain vertex, a point of the lattice on the segment between their vertices.

Algorithms to determine the visible pairs. On the basis of continued fractions and mediant nests of intervals, algorithms were devised by Adler [1] and are reported by Jean [6, p. 39] to determine the visible opposed pairs from a value for the divergence angle d, or to determine an interval of values for d from a visible opposed pair. The proof of Proposition 1 delivers a simpler algorithm to determine all the visible pairs, not just the visible opposed pairs, from the subsequence A of F_N determined by d, and Proposition 5 delivers a simpler algorithm to determine an interval for d from a visible opposed pair. Moreover Adler's definition of visible (opposed) pair is somewhat error-inducing because it is more difficult to apply than the definition of visible pairs given here.

Two types of mechanisms or algorithms can be used to generate all the visible pairs from a value of d and from the corresponding subsequence A of F_N, for any given N: graphical and computational.

1. *Graphical*: from a computer drawing of the strip S corresponding to d and an arbitrary r. We scan the first N points of S with the ray from 0, taking note of the consecutive points. The visible pairs (m, n), $m, n \leqslant N$ are obtained by taking any two consecutive points. The contractions of these pairs are also visible (Proposition 6a). But it is not necessary to use the contractions; we can proceed with the ray from 0 by scanning S for $N=2$, 3, 4, ..., or by using the notion of the fundamental triangle.

2. *Computational*: from the simple computer programme generating and ordering the values $(kd)/k$, $k \leqslant N$. If $nd-[nd]=0.5$, where $[nd]$ is the integral part of nd, then choose both $[nd]$ and $[nd]+1$. Given the values in A their ordering can be made algorithmically by building the appropriate consecutive mediants between 0/1 and $(xd)/x$ where x is the first integer such that $(xd)=1$ (see Example 3).

For a given N, the denominators m and n of the two fractions of A on both sides of the vertical axis, or on both sides of the value of d, represent the visible opposed pair (m, n), whose contractions are the visible opposed pairs corresponding to d and N (Proposition 6b). If d is the rational number p/q, there are two sequences of visible opposed pairs for $N > q$, given that point q is on the vertical axis. If d is irrational, there is only one sequence of visible pairs obtained by taking N as large as any number.

EXAMPLE 2. *Graphical determination of the visible pairs.* For $N = 29$ and $d = 100°$ or $5/18$, scanning Fig. 2 with a ray from 0 gives the following subsequence A of F_{29}:

$$\frac{0}{1}, \frac{1}{5}, \frac{2}{9}, \frac{1}{4}, \frac{7}{27}, \frac{6}{23}, \frac{5}{19}, \frac{4}{15}, \frac{7}{26}, \frac{3}{11}, \frac{8}{29}, \frac{5}{18}, \frac{7}{25}, \frac{2}{7}, \frac{7}{24}, \frac{5}{17}, \frac{3}{10}, \frac{4}{13}, \frac{1}{3}, \frac{1}{2}.$$

The visible pairs, up to $m, n = 29$ are $(1, 5)$, $(5, 9)$, $(9, 4)$, ..., $(10, 13)$, $(13, 3)$, $(3, 2)$ and all the contractions of these pairs. The vertical line in sequence A represents the vertical line through 0 in the lattice or the value of d. The pairs $(29, 18)$ and $(18, 25)$ are visible and opposed, together with their consecutive contractions which are $(11, 18)$, $(18, 7)$, $(11, 7)$, $(4, 7)$, $(4, 3)$, $(1, 3)$, $(1, 2)$. The figure shows that among these contractions the pair $(4, 3)$ is conspicuous (Proposition 7). When d is $1/3 + \phi^{-1}$, an irrational value between $8/29$ and $5/18$, the pairs $(18, 25)$ and $(18, 7)$ are no longer opposed, and we have a single sequence of visible opposed pairs. Notice that point 9, for example, is such that $(9d)/9$ is $2/9$ and $1/3$. Given that Proposition 1 is satisfied for $(9d) = 2$, the pairs $(5, 9)$ and $(9, 4)$ are

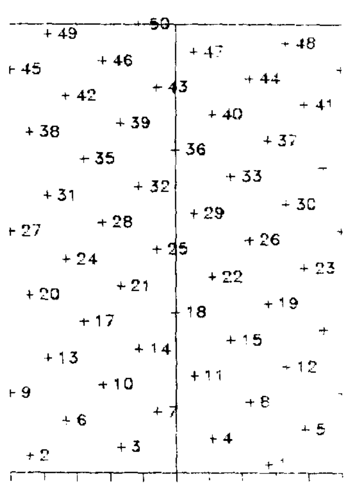

FIG. 2. A rational value for the divergence delivers two sequences of visible opposed pairs, namely $(1, 2)$, $(1, 3)$, $(4, 3)$, $(4, 7)$, $(11, 7)$, followed by $(11, 18)$ and consecutive left extensions $(29, 18)$, $(47, 18)$, ..., or followed by $(18, 7)$ and consecutive right extensions $(18, 25)$, $(18, 43)$, ... The points 9, 27, 45, ... , are considered to be on the right side of the strip S, with a secondary divergence equal to $+\frac{1}{2}$.

visible. The case $(9d) = 3$ gives that point 9 is not even visible from the origin. At the beginning of the 1950's Crick put forward a lattice built on the value 5/18 to represent the pattern of amino-acid residues in polypeptide chains. Jean [7] proposes an analysis of those chains based on the particular case of Proposition 5 mentioned after that proposition, with $t = 3$.

EXAMPLE 3. *Computational determination of the visible pairs.* Let $d = 105°$ and $N = 20$. The computer programme gives the fractions in A:

$$\frac{0}{1}, \frac{1}{2}, \frac{1}{3}, \frac{1}{4}, \frac{1}{5}, \frac{2}{7}, \frac{3}{10}, \frac{3}{11}, \frac{4}{13}, \frac{4}{15}, \frac{5}{16}, \frac{5}{17}, \frac{5}{18}, \frac{6}{19}.$$

For ordering the fractions we insert mediants between 0/1 and 1/2, so as to use all of the fractions consecutively:

$$\frac{0}{1} \;\Big|\; \frac{1}{2},$$

$$\frac{0}{1} \;\Big|\; \frac{1}{3}\;\frac{1}{2},$$

$$\frac{0}{1}\;\frac{1}{4} \;\Big|\; \frac{1}{3}\;\frac{1}{2},$$

$$\frac{0}{1}\;\frac{1}{5}\;\frac{1}{4} \;\Big|\; \frac{1}{3}\;\frac{1}{2},$$

$$\frac{0}{1}\;\frac{1}{5}\;\frac{1}{4}\;\frac{2}{7} \;\Big|\; \frac{1}{3}\;\frac{1}{2},$$

$$\vdots$$

$$\frac{0}{1}\;\frac{1}{5}\;\frac{1}{4}\;\frac{4}{15}\;\frac{3}{11}\;\frac{5}{18}\;\frac{2}{7} \;\Big|\; \frac{5}{17}\;\frac{3}{10}\;\frac{4}{13}\;\frac{5}{16}\;\frac{6}{19}\;\frac{1}{3}\;\frac{1}{2}.$$

The visible opposed pairs are (1, 2) (1, 3), (4, 3), (7, 3), (7, 10), and (7, 17), made with consecutive denominators on each side of the vertical representing d in each row. Values of the rise r can be computed so as to make any of these pairs the conspicuous pair. It can be easily proved that:

PROPOSITION 9. *In any of the rows built according to the above process, for any d, the consecutive visible pairs (m_i, m_{i+1}), $i = 1, 2, ..., k$ (the consecutive denominators in the row) are such that*

$$\sum_{i=1}^{k-1} (m_i m_{i+1})^{-1} = 1/x,$$

where x is the first point of the lattice, after point 1, *on the other side of the vertical axis with respect to point* 1.

For example, in the fourth row here, $(1/5)+(1/20)+(1/12)+(1/6)=\frac{1}{2}$, given that $x=2$ when d is larger than 90 degrees ($x=n$ when d is between $180/n$ and $180/(n-1)$ degrees).

EXAMPLE 4. *Determination of an interval for the divergence.* The following algorithm delivers an interval for d from a visible opposed pair. The algorithm amounts to solving the diophantine equation $|nu-mv|=1$. For example, if the visible pair is (29, 18), it is seen that the possible values for u and v are $u=29p\pm 8$, and $v=18p\pm 5$, where p is any integer. If we are to have $0<u<29$ and $0<v<18$, then we must put $p=1$ ($u=21$ and $v=13$) or $p=0$ ($u=8$ and $v=5$). But only the value $p=0$ gives a divergence smaller than $\frac{1}{2}$, so that the interval for d is [8/29, 5/18].

6. CONCLUSION

The mathematical concepts found in phyllotaxis have been investigated here with Farey sequences. A characterization of the visible pairs has been given, together with a general characterization of the visible opposed pairs. On the one hand those concepts, emerging from a sector of plant morphogenesis, are not dealt with in the theory of Farey sequences, and their introduction therein brings distinctive results. On the other hand the paper briefly reveals the role and significance of Farey sequences in plant biology, by which new results are delivered, known results are made immediate, generalized, and by which we can get rapidly to the consequences of an important trend of investigation in phyllotaxis, along the lines of biologically plausible number-theoretic assumptions formulated in the last century.

APPENDIX: LATTICES IN THE STUDY OF PHYLLOTAXIS

The regular lattice in Fig. 3 is what is called the cylindrical representation of the usual case of phyllotaxis. It shows 8 lines linking the points by eight, 5 lines linking the points by five, and 13 lines linking them by thirteen. The pair (8, 5) is conspicuous given that points 8 and 5 are the closest to 0 (the figure shows in dark lines the parastichy triangle made by this pair, a concept mentioned after Proposition 3). The pairs (5, 8), (8, 13), (13, 21), (21, 34), (34, 55), ..., are visible and opposed, given that the points in each pair are on opposite sides of the vertical axis and that

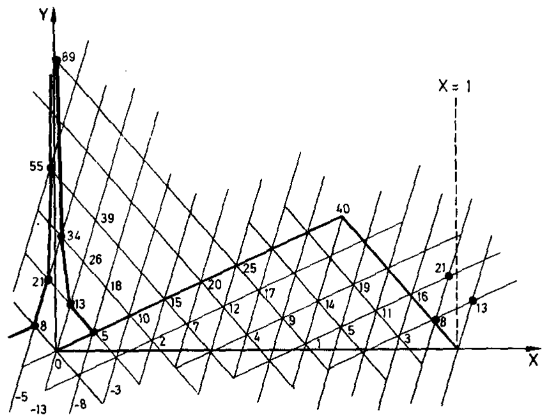

FIG. 3. A lattice obtained by studying pine cones, daisies, sunflowers, cacti, leafy stems, etc. The points represent the florets of the daisies, the leaves on the stem, the needle of the cactus, etc. The horizontal distance between two points is equal to ϕ^{-2} (about 0.382). The consecutive numbers in the Fibonacci series alternate around the vertical axis while getting closer to it, determining two infinite polygonal lines asymptotic to the axis, and containing between them no other point of the lattice. Given that ϕ^{-2} does not have intermediate convergents, there is no point of the lattice on these lines, except those at their vertices.

the triangle made by these points and point 0 contains no other point of the lattice. This is due to the value ϕ^{-2} of the divergence angle of the lattice, the distance between the two vertical lines in the figure being equal to 1. The denominators of the consecutive principal convergents of ϕ^{-2} are indeed precisely 2, 3, 5, 8, 13, 21, 34, 55, 89, ... These numbers are the neighbors of the axis. They alternate on the right and on the left of the axis (in agreement with one of Bravais and Bravais hypotheses mentioned after Proposition 7). This alternation is due to the fact that ϕ^{-2} does not have intermediate convergents. By the decrease of the rise, that is the ordinate of point 1 (that of point n is n times the rise), the conspicuous pair becomes, consecutively, (8, 13), (21, 13), (21, 34), ... The problem of phyllotaxis is to explain why consecutive terms of the Fibonacci series arise almost all the time in the spirals seen on plants.

Rolling up the vertical strip in Fig. 3, so that the two vertical lines coincide, gives a cylinder, and the straight lines of the lattice become helices around the cylinder. These helices can be the ones in the approximately cylindrical pine cone or in the cylindrical stem with the insertions of its leaves, as in Fig. 4. In this figure one can go by the shortest path from leaf 3 to leaf 11, approximately directly above leaf 3, by making 3 turns around the stem and by meeting 8 leaves. The ratio 3/8 is called a phyllotactic fraction (a notion introduced in the second paragraph of Section 2). It is an approximation of the divergence angle of the stem. Notice that 3/8 is pretty close to ϕ^{-2}, the number which when multiplied by 360° gives $137\frac{1}{2}°$, the almost omnipresent divergence angle in plants (3/8 corresponds to 135°). When the stem is seen from above, we get a flat bundle of leaves showing leaves 3, 5, and 8 around leaf 0, as in the lattice of Fig. 3. There too one can draw families of 3, 5, 8, ..., spirals linking the leaves by three, five, eight, ... , respectively. These numbers are also those obtained by counting

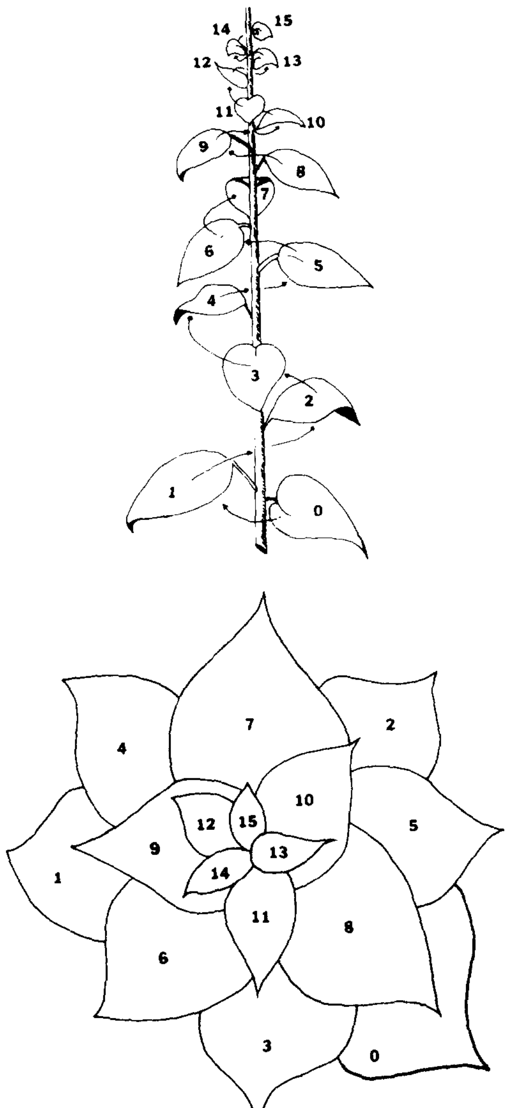

Fig. 4. A leafy stem where the leaves are numbered in their order of appearance. Seen from above the leaves determine families of 3, 5, 8, ..., spirals, and opposed parastichy pairs, such as (5, 3) which is conspicuous. The divergence of the system is also around ϕ^{-2}, or $137\frac{1}{2}°$.

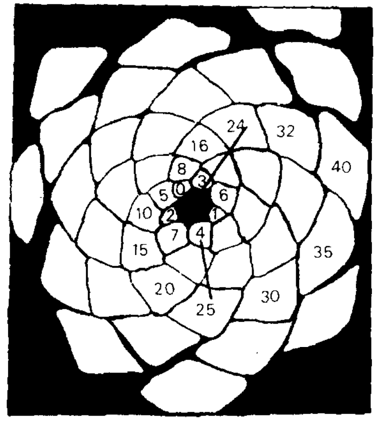

FIG. 5. Transverse section of a pine bud showing the primordia, that is the future scales or needles, arranged in families of spirals. The angle drawn between scales 24 and 25, or between scales n and $n+1$, is equal to about $137\frac{1}{2}°$.

the spirals in a transverse section of the pine bud shown in Fig. 5. The pair (5, 8) is again conspicuous, the eyes being attracted in the directions determined by the quadrangular form of the primordia.

So, smoothly, we go from a regular lattice of points to a display of spirals in the plane. Reversing the process, by a logarithmic transformation of the type $r = \ln R/2\pi$, for example, the ratio R of the distances to the center (e.g., of the cross section in Fig. 5) of two consecutively born primordia, becomes the rise r in the cylindrical lattice. Also the spirals (seen in a bud or in the capitulum of a daisy or of a sunflower) become the straight lines in the regular lattice of points in Fig. 3. In the sunflower the visible opposed pairs are (21, 34) or (34, 55) or (55, 89) or even (89, 144). In the pine cone the pairs are almost exclusively (2, 3), (3, 5), and (5, 8).

When the numbers observed do not belong to the Fibonacci series, they are consecutive members of Lucas series 1, 3, 4, 7, 11, 18, ..., and more generally they are consecutive members of the series 1, t, $t+1$, $2t+1$, $3t+2$, ..., called the series of normal phyllotaxis ($t=2$ gives Fibonacci series, and $t=3$ gives Lucas series). Among the rare case where spiral phyllotaxis is not normal, the series observed is 2, $2t+1$, $2t+3$, $4t+4$, $6t+7$, ..., the series of anomalous phyllotaxis considered in Example 1.

The cylindrical lattice studied in this article is the framework where generally the phenomenon of phyllotaxis is modelled, statically and dynamically. The mathematical study of such lattices allows us to better understand the structure of the phenomena they represent. Phyllotaxis is the first biological phenomenon to be mathematized, well before genetics. Bravais and Bravais biologically plausible assumptions put forward in the text constitute one of the first attempts to explain phyllotaxis. To get acquainted with the theories and models that try to explain the various facts of this important morphogenetic phenomenon (the bugbear of botany), the reader is referred to the authors publications mentioned in the references (especially Jean [5, 6]). Jean [9] presents an updated version of the author's own model.

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